Distribution and dynamics of tree species across a fire frequency gradient in the James Bay region of Quebec

Marc-André Parisien and Luc Sirois

Abstract: This study examines how forest structure and composition change with spatial variations in the fire cycle across a shore–hinterland gradient. Twenty-one well-drained sites were sampled at different distances from James Bay to describe the forest stands. To quantify the role of fire in tree species distribution, a spatial analysis of fire polygons from 1930 to 1998 was undertaken in a 43 228 km^2 study area adjacent to James Bay. Results from this analysis reveal an important decrease in the fire cycle, from 3142 to 115 years, from the shore to the hinterland. In forests bordering James Bay, white spruce (*Picea glauca* (Moench) Voss) is found in pure stands. It is gradually replaced by black spruce (*Picea mariana* (Mill.) BSP) at 0.5 km from the shore. Jack pine (*Pinus banksiana* Lamb.) abruptly appears at 22 km from the shore. There is a positive correlation between the frequency of white spruce and the fire cycle (R = 0.893), whereas this correlation is negative for black spruce (R = –0.753) and jack pine (R = –0.807) (Spearman correlations). Jack pine is confined to regions having a short fire cycle, while black spruce can seemingly maintain itself with or without fire. The exclusion of white spruce hinterland seems to be mainly due to a short fire cycle; however, other factors, such as soil development and species abundance, presumably have a marked influence on the distribution of this species.

Résumé : Le but de cette étude est d'examiner les changements dans la structure et la composition forestières en fonction des variations spatiales du cycle de feux le long d'un gradient de continentalité. Afin de décrire les peuplements forestiers, 21 sites bien drainés ont été échantillonnés à différentes distances de la Baie James. À partir de polygones des feux de 1930 à 1998, une analyse spatiale a été entreprise pour quantifier le rôle des feux dans la distribution des espèces arborescentes dans un secteur d'étude de 43 228 km^2 adjacent à la Baie James. Les résultats de cette analyse révèlent une importante réduction du cycle de feux, de 3 142 à 115 ans, de la côte jusqu'à l'intérieur des terres. Adjacente à la Baie James, l'épinette blanche (*Picea glauca* (Moench) Voss) se retrouve en peuplements purs. Cette espèce est graduellement remplacée par l'épinette noire (*Picea mariana* (Mill.) BSP) à partir de 0,5 km de la côte. Le pin gris (*Pinus banksiana* Lamb.) apparaît brusquement à 22 km de la côte. Une corrélation positive est observée entre la fréquence de l'épinette blanche et le cycle de feux (R = 0,893), tandis que cette corrélation est négative pour l'épinette noire (R = –0,753) et le pin gris (R = –0,807) (corrélations de Spearman). Le pin gris est confiné aux régions ayant un cycle de feux court, alors que l'épinette noire semble pouvoir se maintenir avec ou sans feux. L'exclusion de l'épinette blanche à l'intérieur des terres semble être surtout associée à un cycle de feu court; cependant, on peut présumer que d'autres facteurs, tels le développement des sols et l'effectif de l'espèce, ont une grande influence sur la distribution de cette espèce.

Introduction

At the continental level, plant distribution is largely a function of climate (Woodward 1987), and as climate changes, species distribution changes accordingly (Delcourt and Delcourt 1987). Natural fire regimes are also a function of climate (Filion 1984; Payette and Gagnon 1985; Clark 1988; Swetnam 1993). While plant populations respond rather slowly to changes in climate alone (Davis 1989), their change in distribution is accelerated when fire is involved (Overpeck et al. 1990; Sirois et al. 1994). One would then expect fire-mediated change to be amplified where the extent and magnitude of fire disturbances are important, as is the case in most of the North American boreal forest. This biome has a fire regime in which large and intense fires prevail. In fact, 2–3% of the fires are responsible for 97% of the area burned (Weber and Stocks 1998). A close relationship thus exists between the boreal forest vegetation and the fire regime (Van Wagner 1983), as evidenced by the different fire adaptation strategies of boreal tree species (Rowe and Scotter 1973).

The fire regime describes the nature of fire in an ecosystem and is defined as fire intensity, frequency, timing (season), sizes, severity, and type (Weber and Flannigan 1997). It is well recognized that the fire regime has a marked influ-

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ence on the structure and function of boreal forests (Heinselman 1973). The relationship between the presence of one particular boreal tree species and different aspects of the fire regime has been documented for red pine (*Pinus resinosa* Ait.) (Bergeron and Brisson 1990; Flannigan 1993), jack pine (*Pinus banksiana* Lamb.) (Cayford and McRae 1983; Desponts and Payette 1992; Flannigan and Wotton 1994; Gauthier et al. 1996; Pinard 1999), and black spruce (*Picea mariana* (Mill.) BSP) (Foster 1983; Viereck 1983; Pinard 1999). While many other studies of vegetation describe multispecies dynamics (Cogbill 1985; Johnson and Fryer 1989; Frelich and Reich 1995; Larsen and MacDonald 1998; Bergeron 2000), only some of them consider spatially explicit changes in the fire regime. Changes in the fire regime as a function of latitude (Payette et al. 1989), altitude (Tande 1979), stand type (Larsen 1997), as well as topographical features (Engelmark 1987; Bergeron 1991) have been documented, but rarely as a function of longitude in the boreal forest (but see Bergeron et al. 2001).

The present study examines how forest structure and composition change with spatial variations in the fire regime across a longitudinal shore–hinterland gradient in the James Bay region of Quebec. This sector is virtually free of active fire suppression, and a fire cycle of 109 years has been calculated for a hinterland subset of the sector (Couturier and Saint-Martin 1990). A marked zonation in tree species distribution from the coast to the hinterland (Ducruc et al. 1976; Gérardin 1980) suggests that important spatial variations exist in the factors driving tree species distribution. Our central hypothesis is that, in the study area, longitudinal change (i.e., parallel to the James Bay) in vegetation is mainly associated with change in the fire regime. Conversely, because of the relative uniformity in landform and topography throughout the study area, a weak relationship to the fire regime would indicate that climate or site-specific factors are the main determinants of tree species distribution. This purpose of this study is twofold. First, we document the structure and composition of forest stands, including soil and topographical factors, across two shore–hinterland transects on the eastern side of James Bay. Second, with a database of fire polygons from 1930 to 1998 and GIS technology, we focus on the relationship between tree species distribution and dynamics and the fire regime as a function of distance from the James Bay shore. The role of this and other factors in the forest zonation of the study area is assessed.

Materials and methods

Study area

This study was done in the James Bay region of Quebec in the northern part of the boreal forest region (Rowe 1972). The western edge of the study area is the James Bay coast and it extends 100 km inland from south (51°16′N) to north (54°70′N) for a total area of 43 228 km^2 (Fig. 1). The entire area was used to quantify spatial variations in the fire regime, whereas fieldwork was carried out along two transects, Chisasibi (CH) and Longue Pointe (LP), that extend from the James Bay coast to ≈100 km in the hinterland, around 53°50′N. Lakes and wetlands, which are more or less evenly dispersed throughout the sector, cover about 11% of the territory (Gérardin 1980). The James Bay region is uncommonly flat, although elevations of 250 m above sea level are attained in the eastern part of the study area. The study sector lies in the Precambrian Canadian Shield and its bedrock is composed mostly of granite and gneiss (Stockwell et al. 1968). Podzols and Organosols are the main pedogenetic types throughout. Following the retreat of the Laurentian Ice Sheet approximately 8000 years ago, the postglacial Tyrrell Sea moved in to cover the whole study area (Hardy 1977). Currently, isostatic rebound causes land to rise from the bay at a rate of 1 cm/year (Andrews 1990).

Long, cold winters and short, warm summers characterize the region's low-subarctic climate. From south to north of the study area, the mean annual temperatures range from –1 to –4°C, the coldest and warmest months being January and July, respectively (Environment Canada 1993). The length of the growing season (frost-free) in the southern part of the study area lasts, on average, 140 days with 1100 degree-days ≥5°C, whereas these values are 120 days and 600 degree-days in the northern part (Gérardin 1980). Yearly total precipitation from south to north varies from 700 to 600 mm, about one-third of which falls as snow. The ice-free period of the coastal region is characterized by maritime-type weather, having frequent rainfall events and fog covering the land (Plamondon-Bouchard 1975).

The arboreal vegetation is almost exclusively coniferous, with a small deciduous component increasing in the southern part of the study area. Black spruce is the most common species and is found in a wide range of habitats. Inland, jack pine is often the dominant species on well-drained sites but is generally absent near the coast. Conversely, white spruce (*Picea glauca* (Moench) Voss) is found almost exclusively in coastal areas and more rarely farther inland on stream banks and disturbed sites. Balsam fir (*Abies balsamea* (L.) Mill.) is localized in sites having long fire intervals, whereas balsam poplar (*Populus balsamifera* L.) is sparsely distributed throughout, mainly on alluvial sites. Eastern larch (*Larix laricina* (Du Roi) K. Koch), trembling aspen (*Populus tremuloides* Michx.), and paper birch (*Betula papyrifera* Marsh.) are ubiquitous throughout the study area but are seldom dominant. Understorey vegetation consists largely of ericaceous shrubs, with a forest floor cover of either lichens of the genus *Cladina* or pleurocarpous moss species or both.

Cree natives have inhabited the area for millennia, but there is no evidence of them having used fire for wildlife management or land-clearing purposes. The major anthropogenic perturbation to have occurred in the study area is the creation of immense reservoirs for hydroelectric development. Most of the flooded land, however, is located east of the study area. Therefore, we are working with a natural fire regime in a largely unaltered landscape.

Site selection

The vegetation data was collected during the summer of 1999. Before any sampling was initiated, a thorough area survey was carried out along the two roads leading from Radisson to James Bay: CH and LP. These roads provided easy access to the forest and were thus used as transects. Two methods were used for exploration of the area. The first method was to map the general distribution of species along the entire length of the bay using phytosociological studies (Hustich 1950; Rousseau 1968; Ducruc et al. 1976; Gérardin

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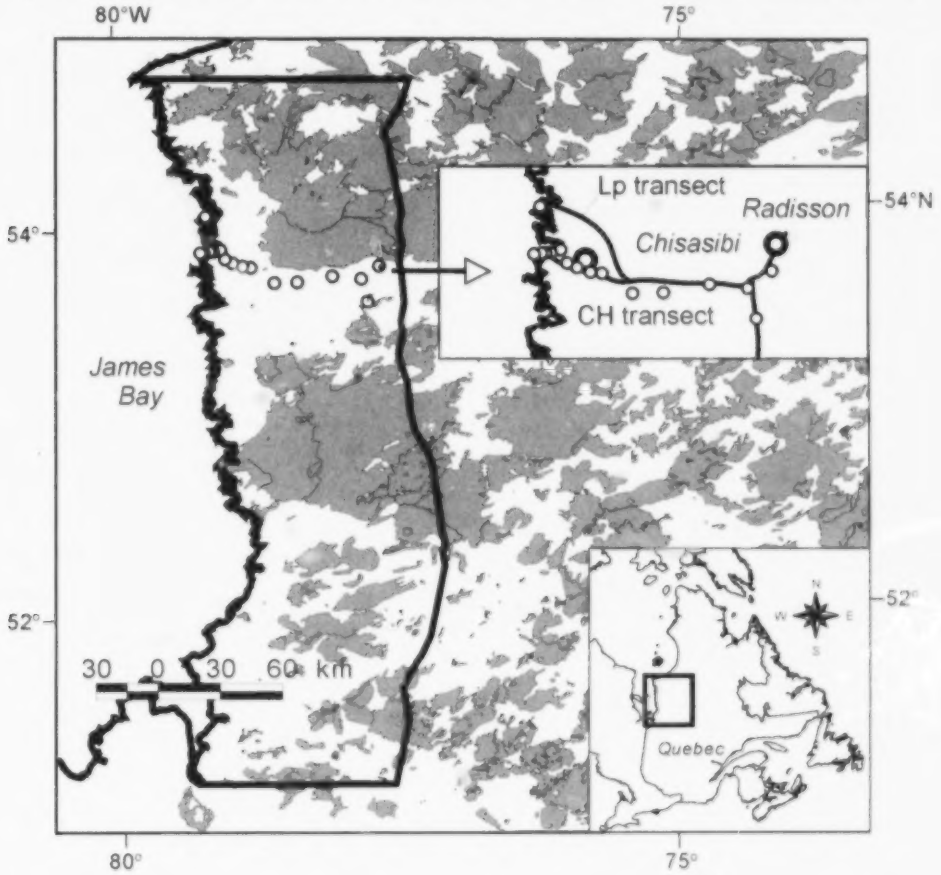
Fig. 1. Location of the study area (outlined) in northwestern Quebec. The grey areas are fires from 1930 to 1998 and the circles represent the 21 sampling stations. Note that near the coast, some circles and small fires are not visible because of circle overlap.



1980). We then undertook a more precise and localized mapping of species distribution along our transects by surveying the area at systematic points 1 km north and south of the roads used as transects. Three distinct vegetation zones based on white spruce (WSp), black spruce (BSp), and black spruce and jack pine (BSp-JPi) abundance were delimited from the coast to the inland (Table 1).

The selection criteria for study sites were drainage class 2 or 3 (Soil Classification Working Group 1998), a weak slope (≤10°), and presence of forest stands well into reproductive age. This last criterion was chosen to set a standard of comparison among zones and because young stands were rare or absent close to the bay. Seven sampling stations were selected in each zone (Table 2) and were distributed at more or less regular intervals within each zone (Fig. 1). Because of its narrowness, stations in the WSp zone were located in both transects, whereas stations for the two other zones were only set up on the CH transect. To determine the age of potential stands, fire scars were collected, polished, and dated using a dissecting microscope (25–40×) before the selection of a sampling station was made.

Table 1. Longitudinal vegetation zones as delimited at approximately 53°30′N on the eastern side of the James Bay.

Zone	Dominant tree species	Distance from the coast (km)	Area (ha)
WSp	White spruce	0–0.5	53 946
BSp	Black spruce	0.5–22	1 037 369
BSp-JPi	Black spruce and jack pine	22–100	3 231 474

Vegetation and soil sampling

In each station, vegetation was sampled in ten 10 × 10 m sampling plots that were at least 20 m from one another. When stem densities were low (<100), the number of sampling plots was increased up to 15 and in one case (BSp-5) was reduced to eight because of extremely high densities.

Tree species were classified as either trees (height >1.5 m) or saplings (≤1.5 m). Diameter and height of every individual tree, dead or alive, were measured at 1.40 m (diameter at breast height (DBH)) and their height estimated with a clinometer. At each station, 15–30 randomly selected trees of each species were cored at 30 cm above ground (except for WSp-1 and WSp-2, which had very few trees). The age of the trees was determined later by core analysis conducted in the laboratory. Basal age was obtained by adding the differ-

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Table 2. Name, transect, distance from the James Bay coast, and year of the last fire of the 21 sampling stations used for characterizing tree species distribution and dynamics along a shore–hinterland gradient in the James Bay area.

Station	Transect	Distance from the coast (km)	Year of last fire
WSp-1	LP	0.075	No trace of fire
WSp-2	LP	0.2	No trace of fire
WSp-3	LP	0.275	No trace of fire
WSp-4	LP	0.45	No trace of fire
WSp-5	CH	0.05	No trace of fire
WSp-6	CH	0.15	No trace of fire
WSp-7	CH	0.2	No trace of fire
BSp-1	CH	0.75	1938
BSp-2	CH	1.25	1938
BSp-3	CH	4.15	1938
BSp-4	CH	6	1937
BSp-5	CH	8	≈1775
BSp-6	CH	11	1881
BSp-7	CH	17	1857
BSp-JPi-1	CH	22	1932
BSp-JPi-2	CH	31	1940
BSp-JPi-3	CH	44	1941
BSp-JPi-4	CH	63	1940
BSp-JPi-5	CH	78	1923
BSp-JPi-6	CH	80	1941
BSp-JPi-7	CH	90	1921

Note: LP, Longue Pointe; CH, Chisasibi.

ence in mean ages at 0 and 30 cm counted from disc samples ($n \approx 30$) for all species in the three vegetation zones.

The saplings' base diameter and height were measured. Whether their origin was from seed or layering was also noted. They were also labelled and brought to the laboratory for age determination. These data, however, will be analysed elsewhere, with the exception of BSp-JPi-6, which had an atypical regeneration pattern. In addition, for all BSp-JPi stations, the proportion of open cones was estimated for 10 dominant individuals.

Percent cover was visually estimated for tree species. A detailed description of the vegetation assemblages is available in Parisien (2002). Soils were classified according to the Soil Classification Working Group (1998). One soil profile per station was examined to determine soil type and measure the depth of organic and mineral horizons. Soil texture was determined with a sensorial test (Kimmins 1997). Also, soil samples from the B-horizon were brought back to the laboratory and put in a $CaCl_2$ suspension to determine pH (McKeague 1978).

Spatial variations of the fire regime

A digitized database consisting of the polygons of all the fires ≥14 ha from 1930 to 1998 was provided by the ministère des Ressources naturelles du Québec. Fires were classified on a yearly basis between 1972 and 1998 and in 5- to 10-year age-classes prior to 1972. Most fires occurring since 1972 were mapped during or not long after they burned, usually by on-site observations, but also using remote sensing, and are therefore more precise. It is likely that some fires of the early years were not recorded, but the extent of this shortcoming is unknown. Despite this limitation, the database is assumed the best available.

To evaluate the longitudinal variations in the fire regime, a spatial analysis was undertaken using ArcView GIS (Environmental Systems Research Institute 1999). The fire cycle was considered to be the most appropriate index for our analysis of spatial variations in the fire regime. Fire cycle was calculated using Heinselman's (1973) method, the reciprocal of the average percent annual area burned. In ArcView GIS (Environmental Systems Research Institute 1999), the study area was subdivided into narrow strips, 0.5 km for the first 12 km (400–500 km^2) and 1 km for the remainder of the study area (800–900 km^2), parallel to the coastline in which the fire cycle was computed. The outputs from these analyses were also averaged per vegetation zone.

Finally, we used Van Wagner's (1978) negative exponential model to estimate the distribution of stand ages at different distances from the coast. This model uses fire cycle as an input variable and states that 63.2% of stands should be younger than the mean age, which is equal to the fire cycle, if the fire frequency is constant and independent of stand age. Up to a given age (x), the cumulative proportion of stands is described by

$$[1] \qquad \sum f(x) = 1 - e^{-px}$$

where p is the annual probability of fire, which is equal to 1/fire cycle. This distribution was calculated for stands up to 125 years, which is considered the maximum longevity that jack pine persist in the study area (Pinard 1999).

Relationship between sampling stations and explanatory variables

A multivariate analysis, nonmetric multidimensional scaling (NMDS), was performed to assess the similarity between sampling stations based on tree species importance value and explanatory variables. For each sampling station, the importance value was defined as the relative basal area of each tree species, a method allowing comparison between stands of different levels of canopy openness. The other variables used in this analysis were length of the fire cycle, time since the last fire, elevation, soil pH, organic horizon thickness, and Ae horizon thickness. As no trace of fire was detected in the WSp zone, the time since fire was arbitrarily set as 250 years, which is approximately the time since this zone has risen above sea level. To allow us to evaluate relative differences between stations, each variable was standardized by dividing its value at each station by the total for that variable. Other variables, such as slope, aspect, surficial deposit, and texture, were omitted from this analysis because of their relative uniformity throughout sampling stations. Spearman correlation matrices were created with these data. The NMDS ordination method was then carried out for the importance values and explanatory variables as well as for the sampling station by simply transposing the data. The NMDS produced a diagram with two axes (dimensions) having the same weight and where the differences between points are proportional to the distance that separates them.

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Table 3. Mean (±SE) of population structure characteristics for the common tree species of each vegetation zone.

Zone	Species	Mean diameter of trees (cm)	Mean height of trees (m)	Density (stems/ha)	Frequency (%)*	Basal area (m^2/ha)	Age correction 0–30 cm (years)
WSp	White spruce	9.5±2.1	5.2±0.9	1960±244	100.0	15.6±4.9	9
BSp	White spruce	6.0±3.3	4.3±1.2	260±204	32.4±16.0	0.4±0.3	6
	Black spruce	5.0±0.6	4.0±0.4	3566±1184	96.2±2.9	8.6±3.1	8
	Eastern larch	3.5±1.3	5.6±1.0	226±82	56.9±8.8	0.3±0.1	4
BSp-JPi	Black spruce	4.9±0.5	4.5±0.3	5831±2768	88.6±11.4	6.3±2.0	6
	Jack pine	10.0±1.4	6.5±0.5	763±350	81.2±10.9	4.0±0.9	3
	Eastern larch	6.1±1.9	5.1±0.7	70±53	22.9±11.5	0.4±0.4	3
	Trembling aspen	2.5±0.4	3.1±0.2	40±21	19.7±8.4	0.02±0.01	2

*Percentage of sampling plots that contain at least one individual of the species.

Results

Forest structure and composition

White spruce was the only tree species present in the WSp zone. Although highly variable, tree density in this zone was the lowest of the three zones; basal area was the highest because of the presence of some very big trees (Table 3). This zone has only recently (<250 years) risen above see level (based on isostatic rebound curves from Hillaire-Marcel and Vincent 1979); therefore, much of the variation in forest structure was related to the distance from the shore, in turn a function of the time since the land has been exposed. This was evident in the four stations of the LP transect (Fig. 2, WSp-1 to WSp-4): as we move away from the coast, from 0.075 to 0.45 km, the trees get bigger and older and the sites had a higher proportion of dead trees, many of which had fallen down. On the analogous stations of the CH transect (Fig. 2, WSp-5, WSp-6, and WSp-7), the same pattern occurred between WSp-5 (0.05 km) and WSp-6 (0.15 km) but not between the latter and WSp-7 (0.2 km), although WSp-7 did have a greater proportion of dead trees. The lack of difference in forest structure between WSp-6 and WSp-7 was imputable to the smaller age difference between those two stations. The average slope is markedly higher at LP (1.97°) than at CH (0.67°), and thus, the time since the land rebounded above sea level per unit distance was lower at CH than at LP. Also particular to this zone was the high proportion of fallen trees, creating gaps in which young individuals could establish. This phenomenon is again related to distance from the shore; for example, fallen trees represented 50% of the dead trees in WSp-3 and 71% in WSp-4.

The BSp zone is a transition zone between the continental (BSp-JPi zone) and maritime forest (WSp zone). White spruce was present in this zone (Table 3) but gradually disappeared as distance from the bay increased (Fig. 3). White spruce was only found in significant densities in the stations adjacent or close to the WSp zone such as BSp-1, BSp-2, and BSp-4 (Fig. 3). Furthermore, at the easternmost station where it was sampled, BSp-4, white spruce was almost exclusively represented by mature individuals. During our surveys, this species was seen much farther inland than the BSp-4 station, where it persists on riverbanks. Black spruce was by far the most abundant species in the BSp zone (Table 3). It was noted during the area surveys that most stands in this zone were seemingly old (>100 years). While tree diameters roughly followed a negative exponential curve, they are a poor indicator of the age of trees (Fig. 3). Typical of old black spruce stands, a large fraction of the saplings in the older stations (Fig. 3, BSp-5, BSp-6, and BSp-7) originate from layering. In this zone, as well as in the BSp-JPi zone, eastern larch was ubiquitous but never reached great densities; a few trembling aspen individuals were also tallied.

The most obvious difference between the BSp-JPi zone and the two previous zones is jack pine's abrupt appearance and dominance (with black spruce) at 22 km from the coast. Having exhaustively searched the area around both transects, we are fairly confident that at this latitude, jack pine does not occur closer to the bay, as observed by Hustich (1950). On mesic sites of the BSp-JPi zone, jack pine was either the only species present, as in BSp-JPi-6 (Fig. 4), or, more commonly, in varying proportion with black spruce (Fig. 4, all other stations). Although outnumbered by black spruce in several mature stands, jack pine's basal area was comparable with that of black spruce because the trees were bigger (Table 3). Jack pine populations were also markedly different from black spruce populations: the ratio of trees to saplings is higher. An exception was the BSp-JPi-6 station, where most jack pine trees had a diameter less than 2 cm (Fig. 4). Further observation revealed that 87.4% of these small individuals were between 10 and 25 years old in BSp-JPi-6. Concurrently, the proportion of open cones in this stand was higher (16%) than the average for the other BSp-JPi stations (7%). As in the BSp zone, black spruce diameter structures followed a more or less negative exponential distribution; the noticeable difference was that old-growth stands (>100 years) on well-drained sites are scarce in this zone, as noted during our area surveys. The diameter structure of black spruce was, therefore, similar regardless of stand age but had much less layering in the BSp-JPi zone. Eastern larch and aspen were also found in the BSp-JPi zone, but never in great numbers, while three balsam fir trees were tallied in BSp-JPi-1. Unexpectedly, white spruce individuals were found in ditches ploughed about two decades ago, close to BSp-JPi-1.

Soil texture did not differ much among zones, being mostly sands or loamy sands. However, soil pH was significantly lower for the BSp zone ($p < 0.05$, Kruskal–Wallis test

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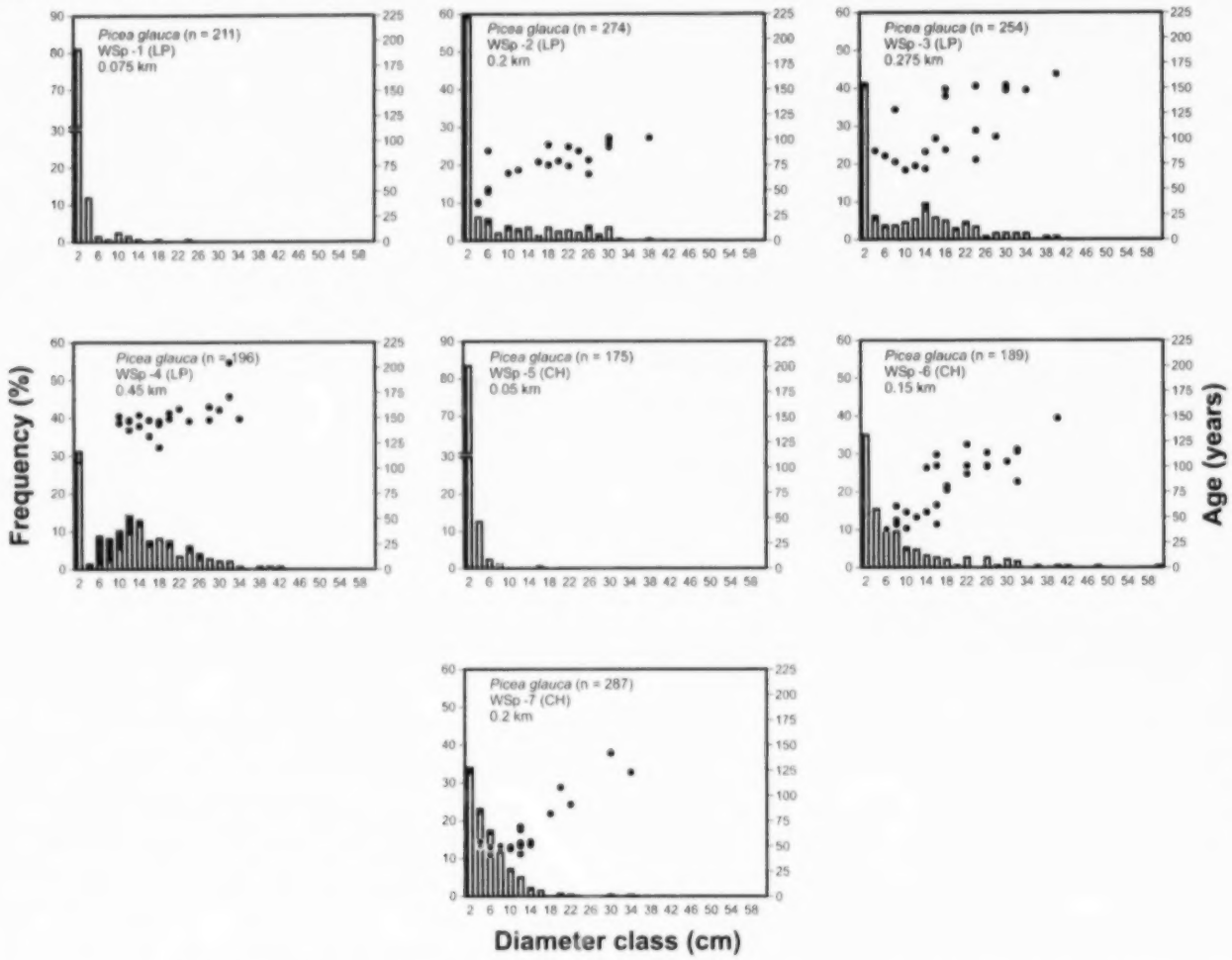
Fig. 2. Distribution of diameter classes (2-cm classes) for live (open bars) and dead individuals (solid bars) as well as layers (shaded bars) for tree species representing 5% or more of stems at each station in the WSp zone. Circles are the ages of cored individuals. Note the different left *y* axis for WSp-1 and WSp-5.



followed by the Wilcoxon rank sum test for independent samples) than for the WSp and BSp-JPi zones. In addition, the BSp-JPi zone had a thinner organic soil horizon and a thicker Ae (eluviated) horizon ($p < 0.05$) (Fig. 5), an index of soil podzolization.

Fire cycle and stand age distribution

There is a marked shortening in the fire cycle as we move away from the James Bay coast, which approximates a negative exponential function (Fig. 6). When averaged per vegetation zone, the fire cycle was 3142, 495, and 115 years for the WSp, BSp, and BSp-JPi zones, respectively. Interestingly, the fire cycle starts levelling off where the BSp-JPi zone begins. In the BSp zone, the fire cycle decreases eastward from 3218 to 330 years. A strong correlation was observed between the frequency of white spruce and the length of the fire cycle as calculated in Fig. 6 ($R = 0.893$), while the frequency of black spruce ($R = -0.753$) and jack pine ($R = -0.807$) decreases as the fire cycle increases (Spearman correlations).

The estimated proportion of stands that are 125 years or younger derived from the fire cycle values expectedly show a strong eastward increase (Fig. 7). The estimated parameter is very sensitive to small changes in fire cycle values because of the nature of Van Wagner's (1978) model (i.e., exponential); hence, the lack of smoothness in the curve.

Ordination of sampling stations and explanatory variables

Correlations between explanatory variables and the axes (Table 4) show that the first axis of the NMDS (Fig. 8) is mainly a function of the fire variables (especially fire cycle)

Fig. 3. Distribution of diameter classes (2-cm classes) for live (open bars) and dead individuals (solid bars) as well as layers (shaded bars) for tree species representing 5% or more of stems at each station in the BSp zone. Solid circles are the ages of cored individuals, and the year of the last fire is shown at the top. Open circles are the ages of cored trees older than the last fire. Note the changes in both *y* axes.

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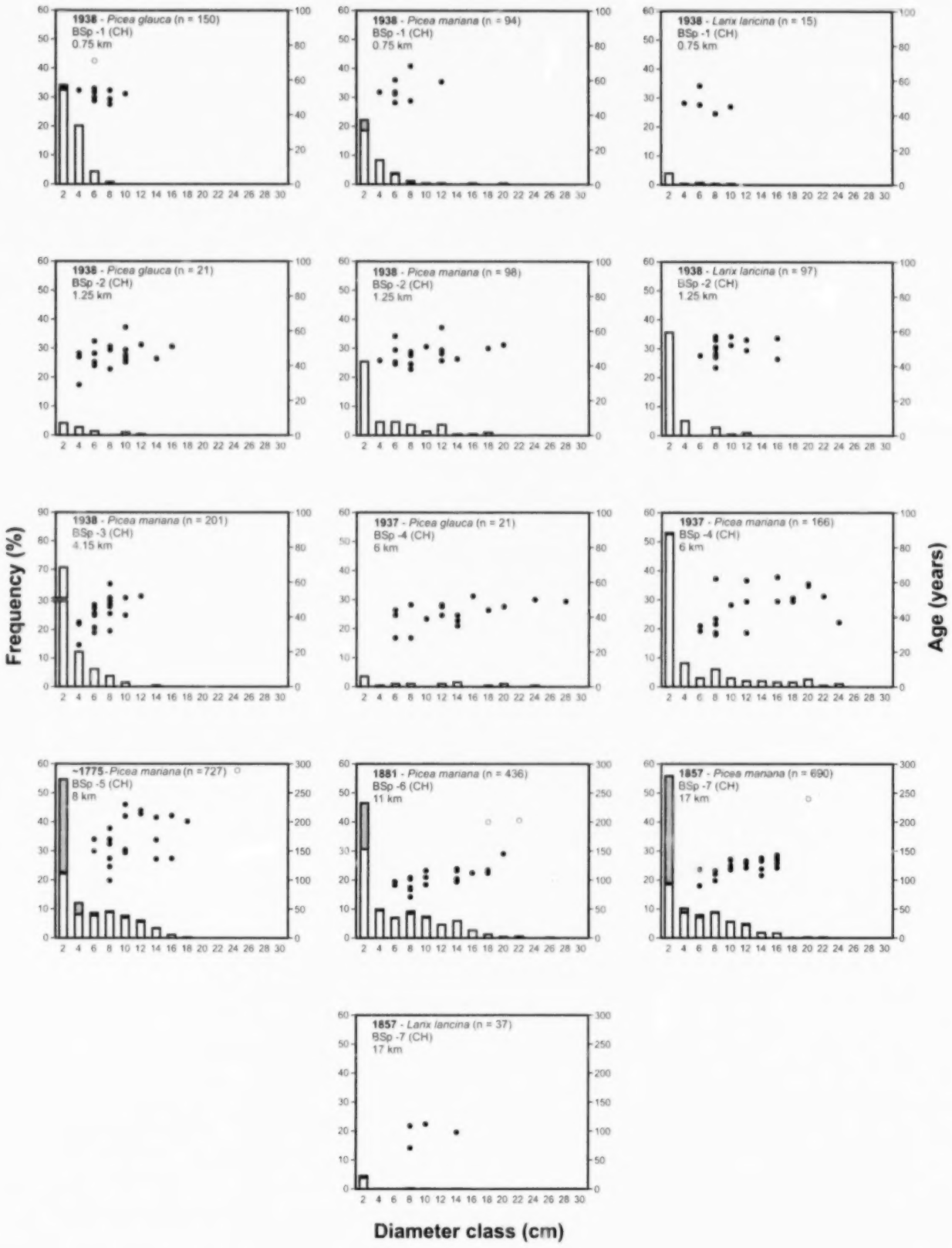

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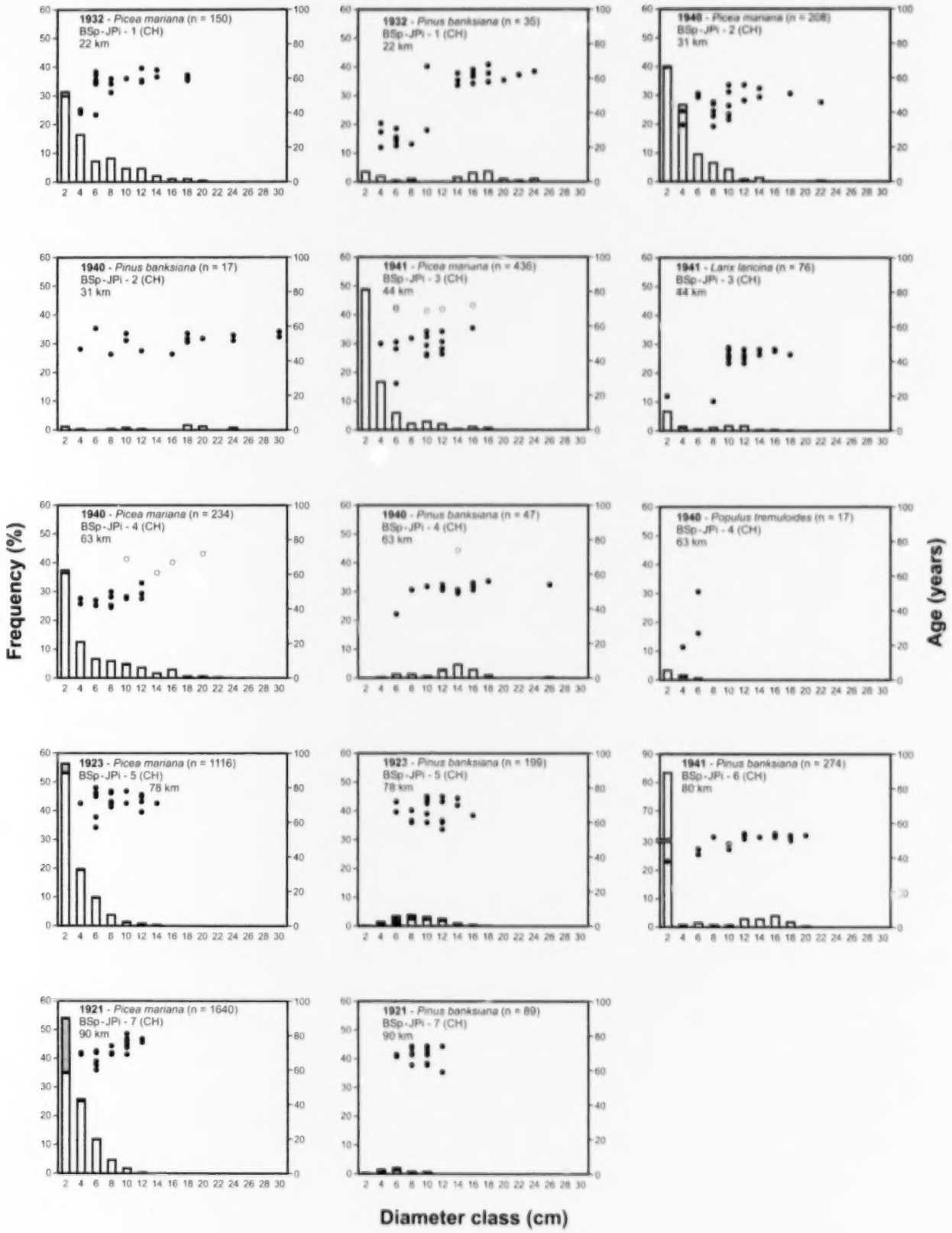
1932 - Picea mariana (n = 150)
BSp-JPi - 1 (CH)
22 km
1932 - Pinus banksiana (n = 35)
BSp-JPi - 1 (CH)
22 km
1948 - Picea mariana (n = 208)
BSp-JPi - 2 (CH)
31 km
1940 - Pinus banksiana (n = 17)
BSp-JPi - 2 (CH)
31 km
1941 - Picea mariana (n = 436)
BSp-JPi - 3 (CH)
44 km
1941 - Larix laricina (n = 76)
BSp-JPi - 3 (CH)
44 km
1940 - Picea mariana (n = 234)
BSp-JPi - 4 (CH)
63 km
1940 - Pinus banksiana (n = 47)
BSp-JPi - 4 (CH)
63 km
1940 - Populus tremuloides (n = 17)
BSp-JPi - 4 (CH)
63 km
1923 - Picea mariana (n = 1116)
BSp-JPi - 5 (CH)
78 km
1923 - Pinus banksiana (n = 199)
BSp-JPi - 5 (CH)
78 km
1941 - Pinus banksiana (n = 274)
BSp-JPi - 6 (CH)
80 km
1921 - Picea mariana (n = 1640)
BSp-JPi - 7 (CH)
90 km
1921 - Pinus banksiana (n = 89)
BSp-JPi - 7 (CH)
90 km
Frequency (%)
Age (years)
Diameter class (cm)

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Fig. 4. Distribution of diameter classes (2-cm classes) for live (open bars) and dead individuals (solid bars) as well as layers (shaded bars) for tree species representing 5% or more of stems at each station in the BSp zone. Solid circles are the ages of cored individuals, and the year of the last fire is shown at the top. Open circles are the ages of cored trees older than the last fire. Note the different left *y* axis for BSp-JPi-6.

Fig. 5. Organic horizon thickness, Ae horizon thickness, and soil pH in vegetation zones ($n = 7$ for each zone). The box represents the 25th and 75th percentiles and the median (line within the box), the whiskers represent the 10th and 90th percentiles, and the square represents the mean. Different letters indicate significant differences ($p < 0.05$). The organic layer comprises both the LFH and the O horizons.

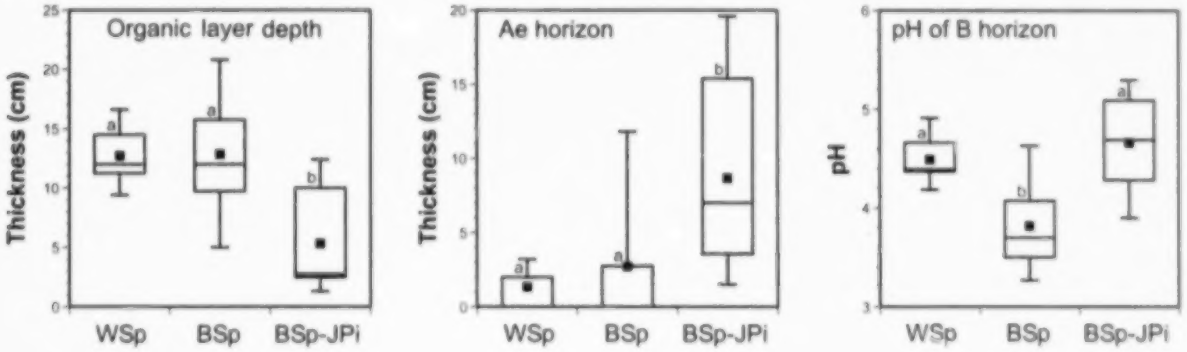


Fig. 6. Fire cycle as a function of distance from the James Bay coast.

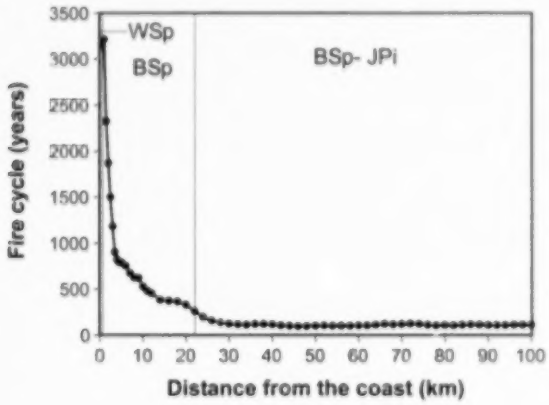
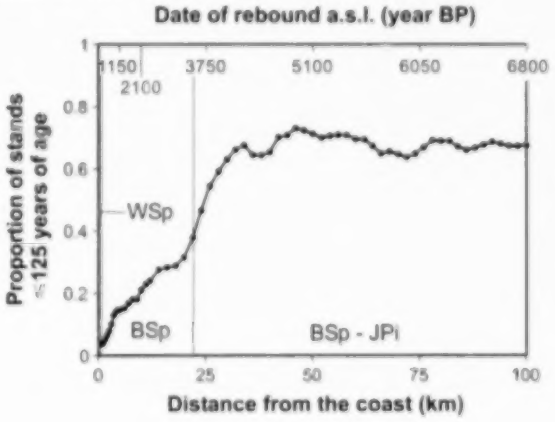


Fig. 7. Proportion of stands of 125 years of age or less as a function of distance from the coast. The upper *x* axis represents the date that land rebounded above sea level at different distances from the coast (modified from Hillaire-Marcel and Vincent 1979).



and elevation, whereas the second axis is mainly related to soil factors. The root mean squared residuals, a measure of variance, indicated that fire cycle and time since fire were the overall most influential explanatory variables of tree species distribution (Table 4). While these two variables appear to covary (Fig. 8), this is not the case, as their correlation is not particularly strong ($R = 0.66$ (Spearman correlation), also apparent from Figs. 2, 3, and 4); furthermore, time since fire is site specific, whereas fire cycle is distance specific. The sampling stations were clearly grouped between zones (Fig. 8), albeit with much scatter for the BSp and BSp-JPi zones, indicating higher variability among the stations of these zones. Dispersal of sites in the NMDS ordination suggests that fire cycles, elevation, and fire intervals, in that order, were the main determinants of forest zonation observed in the field.

Discussion

Individual species dynamics

White spruce

In the WSp zone, where fire is infrequent, the coastal white spruce forest exhibits a gap dynamics in which fallen trees accounted for much of the mortality and subsequent seedling recruitment. The structure of stands in this zone seemed to be dependent of the time since the land has risen above sea level (Fig. 2), as observed by Ricard and Bégin

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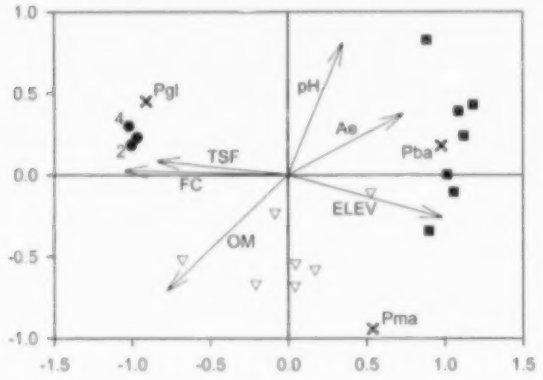
Table 4. Correlation (correlation coefficient) of the nonmetric multidimensional scaling variables with the ordination axes as well as their root mean squared residuals (RMSR).

Variable	Axis 1 (*x* axis)	Axis 2 (*y* axis)	RMSR
Fire cycle length	–0.959	0.025	0.058
Time since fire	–0.768	0.078	0.050
Soil pH	0.318	0.737	0.025
Organic matter thickness	–0.710	–0.649	0.038
Ae horizon thickness	0.672	0.340	0.032
Elevation	0.897	–0.238	0.034

Fig. 8. Nonmetric multidimensional scaling of the 21 sampling stations in the WSp (circles), BSp (triangles), and BSp-JPi (squares) zones based on the importance values (crosses) of white spruce (Pgl), black spruce (Pma), and jack pine (Pba) as well as the variables (arrows) with the following codes: FC, fire cycle length; TSF, time since fire; pH, soil pH; OM, soil organic layer thickness; Ae, thickness of the Ae horizon of soil; ELEV, elevation. The numbers next to the WSp stations indicate the number of overlapping stations.



(1999), whereas in the hinterland, the diameter structure was related to the time since the last fire.

As is the case for the Hudson Bay sector of Quebec (Payette 1975), white spruce forms the maritime tree line along the James Bay (our WSp zone). In both the Hudson and James bays, as land is exposed, the coastal region undergoes primary succession in which the later stages are characterized by the establishment of white spruce in alder thickets, providing nitrogen input and increased snow protection (Ricard and Bégin 1999; Doran et al. 2001).

As we move east of the WSp zone, fires begin "biting" into the forest matrix, thereby creating a narrow (<0.5 km) transition area between white and black spruce dominance. White spruce is ill-adapted to frequent fires compared with black spruce and jack pine, and we believe that this transition is made possible by the very low occurrence of lethal fires. In fact, our results suggest that frequent hinterland fires restrict the eastern expansion of white spruce. In the southern boreal forest of eastern Canada, white spruce is generally a late-succession species, which limits its abundance when the fire interval is short (Bergeron and Dansereau 1993; Bergeron 2000). In western Canada, however, some authors reported that white spruce could remain dominant even in very short mean fire intervals (Johnson 1981; Larsen and MacDonald 1998). It is unclear why this species has such divergent dynamics in different parts of the country, but the much higher abundance of white spruce in western Canada certainly accounts for a higher probability of colonization of newly available sites.

In the boreal forest, white spruce reportedly prefers poorly developed, base-rich (unleached) soils (Ritchie 1957; Engstrom and Hansen 1985; Liu 1990). Our results are consistent with those of Nichols (1976), Lamb (1980), and Engstrom and Hansen (1985), who found that white spruce was the first species to colonize the newly available landscapes. It is impossible to determine from our results to what extent soils are responsible for white spruce dominance near the bay. Unlike Hustich's (1950) observations near the coast (CH transect), we found no relationship between soil texture and the presence of white and black spruce. The white spruce found farther inland, on the nutrient-rich banks of streams and rivers, probably persists in these areas because of low fire occurrence as well as favourable soil conditions. In this respect, these remote sites were similar to the WSp zone. In James Bay, hinterland white spruce is more of a relict than a late-successional species, as reported by Viereck (1983) for the floodplains of Alaska. As the land rebounded and the Tyrrell Sea retreated to the west, our entire sector was, at a given time, close to the bay (Fig. 7, upper *x* axis). It is then highly possible that all sections of the study area had a period of long fire cycle and, accordingly, white spruce dominance. Along our transects, this species was rarely found on well-drained sites >10 km from the coast, even though fire intervals were very long up to the BSp-JPi zone (22 km), which lead us to believe that, to persist in the James Bay landscape, white spruce requires a combination of (*i*) a long fire cycle, (*ii*) favourable soil conditions (i.e., young soils), and (*iii*) close proximity to a metapopulation.

Black spruce

Unlike the WSp zone, all stands where black spruce was sampled had evidence of fire. The distribution of this species near the coast suggests that it appears during postfire succession. At the interface of the WSp and BSp zones, the mechanisms associated with the replacement of white spruce by black spruce are presumably a function of the species' ability to regenerate after a fire, which is influenced by climate and weather, fire interval, edaphic preferences, and species abundance. In the Hudson Bay lowlands, this replacement has been attributed mainly to paludification (Ritchie 1957), whereas in the study area, fire seems to play a determinant role. Black spruce's semiserotinous cones provide the species with an aerial seed bank that releases an impressive number of seeds following fire (Zasada et al. 1979; Black and Bliss 1980). This species is thus able to rapidly colonize after a fire (Morneau and Payette 1989; Saint-Pierre et al. 1992; Sirois 1995). Furthermore, as we move away from the coast, the white to black spruce ratio decreases, exerting a positive feedback and further favouring black spruce establishment. This phenomenon is amplified through time, as the isostatic uplift likely causes the bay's climatic influence to decrease at any given point, which could translate into a westward shift in all vegetation zones.

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In the BSp zone, black spruce was present on all well-drained sites, regardless of the time since fire, thereby creating a monospecific mosaic of different stand ages. Acidic soils resulting from long fire intervals are likely a factor that favours black spruce, which can thrive in low-pH conditions. Indeed, the old forests of the BSp zone have a thick organic layer (i.e., mainly as *Sphagnum* sp. peat accumulation), which is responsible for the lower pH in this zone (Fig. 5), as *Sphagnum* sp. efficiently binds base cations (Clymo 1963). Although there is also a marked increase in pH after a fire, it does not last more than a few years (Gorbachev and Popova 1996). Acidity is thus probably more influenced by organic matter accumulation than actual time since fire. Old-growth stands in the James Bay area therefore promote the exclusion of species other than black spruce, which acts as a late-successional species. In contrast with the BSp zone, where fires are still infrequent, in the BSp-JPi zone, black spruce stands on well-drained sites did not attain old-growth status and almost always had a jack pine component. In the sampled stands of the BSp-JPi zone, jack pine and black spruce both seemingly established immediately after a fire, as suggested by similar ages of cored trees of both species (Fig. 4).

Jack pine

In the study area, the dynamics of jack pine generally correspond to its classic population model (Desponts and Payette 1992; Saint-Pierre et al. 1992; Sirois 1995), where most individuals are part of a single cohort resulting from rapid postfire establishment (Fig. 4). This model stipulates that because of its adaptations to fire, a high recurrence of fire is required for jack pine to thrive on a large spatial scale. For example, because of its serotinous cones, fire intervals shorter than the individuals tree's life span (≈125 years in our sector) are required to release seeds and allow regeneration. Likewise, the removal of organic matter and the increase in pH resulting from a fire also favour jack pine regeneration (Herr and Duchesne 1995). At its northern limit in Quebec, approximately 200 km north of our study sector, Desponts and Payette (1992) found a strong relationship between fire occurrence and the presence of jack pine. In the study area, where jack pine had much stronger regeneration potential than black spruce (Sirois 1995; Lavoie and Sirois 1998), it has been suggested that only a very sparse jack pine component in stands up to 125 years old can ensure its presence and even dominance following fire (Pinard 1999). In fact, Lavoie and Sirois (1998) reported that a large-scale shift in dominance from black spruce to jack pine is a common hinterland feature after large fires in this sector.

We believe that a long fire cycle is responsible for the absence of jack pine near the James Bay coast, as is the case beyond the northern species' limit in Quebec (Desponts and Payette 1992). While fire cycle length determines jack pine distribution at the regional level, time since fire, which is inextricably related to the fire cycle, controls the species' presence locally, as long as the proportion of young stands is high. Even though we realize that our calculation of the proportion of stands up to 125 years (Fig. 7) is an estimate subject to many inaccuracies, it is intended to illustrate the relative scarcity of young stands where jack pine is seemingly absent. In contrast, most BSp-JPi stands (≈70%) are young enough to support jack pine and its abrupt appearance is likely due to the rapid shortening of the fire cycle as well as widespread recruitment after a fire.

The patterns that have emerged at the landscape scale alone cannot explain the distribution of tree species: site-specific differences also play an important role. As observed at the BSp-JPi-6 station, a pure jack pine stand, an atypical second cohort consisting of very small individuals, was recorded (Fig. 4, BSp-JPi-6). The BSp-JPi-6 site is a very open stand resulting from a particularly severe fire, and sunlight penetrates the forest, probably exposing the cones of regenerated trees to high temperatures, which increase the rates of opening of cones (Arseneault 2001). Given the age of the individuals with a DBH of less than 2 cm, most of the cones would have opened when the trees had a much smaller diameter. These results would be in agreement with Gauthier et al. (1993) who determined that young (<10 cm DBH) cone-bearing individuals often exhibit reduced serotiny.

Forest zonation and spatial variations in the fire regime

This study focused on the current forest zonation east of the James Bay. As the topography and land use are similar throughout the studied transects, linking forest structure to areas of contrasted fire regime allows us to draw some conclusions about how various landscapes' vegetation could change when submitted to different fire cycles. It must be noted that conclusions relate to the transect areas and should not be extrapolated to the entire region of the eastern coast of James Bay. A longitudinal zonation does exist along the entire length of the bay (Gérardin 1980) but different vegetation assemblages also occur because of, notably, considerable change in latitude. It is also worth noting that the accuracy of estimating fire cycles decreases as we move towards the bay. A fire chronology two or three times the length of the fire cycle is needed to obtain a reliable estimate of this parameter (Reed et al. 1998; Johnson and Gutsell 1994). Furthermore, because the land is constantly rebounding, the fire regime at a given location is shifting, causing the stand age distribution to be out of equilibrium with the fire cycle in areas under the bay's influence (i.e., the WSp and BSp zones). We are thus well aware that computation of the cumulative proportion of stands up to a certain age is an inaccurate exercise, especially in the WSp and BSp zones. Baker (1992) reported, however, that the mosaic of stand ages moves rapidly towards equilibrium with changes in the fire regime. We believe that our data set (records for 69 years) and the considerable size of the study area (>40 000 km^2), as well as the fact that we are working with a natural fire regime, clearly demonstrate how spatial variation in the fire regime is linked to the marked longitudinal differences in the forest landscape.

Even though a climatic control of tree species distribution is possible across the shore–hinterland gradient, notably at the reproductive level (Sirois et al. 1999), Kinnard (1998) detected no significant differences in radial growth patterns of black spruce on a shore–hinterland gradient in the study area. Although site-specific factors indeed have an effect on forest zonation, particularly at a local level, large-scale vegetation changes are mainly fire mediated in the study area. There is little doubt, however, that the spatial variations in the fire regime are a direct response to climatic processes. In

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the study area, the variations are most likely attributable to the sea breeze effect, which blows moist cold air inland during the fire season, thereby rendering the conditions less conducive to fire ignition and spread in the WSp and BSp zones. Unfortunately, there are no weather data available at this time to verify the existence of a sea breeze effect. Less area burned near the coast might also be due to the fact that the sea breeze "pushes" fires away from the coast at the time of maximum spread (fires generally burn from west to east near the coast; see Fig. 1).

As land rises from the bay, it is conceivable that the zones described herein shift westward and will continue to do so until isostatic equilibrium is reached. The rate at which species migrate longitudinally, however, is very difficult to assess because (*i*) we are uncertain whether species are still in expansion, as jack pine presumably is (Richard 1979; Lavoie and Sirois 1998), or in decline in our sector, (*ii*) it is impossible to know if the bay's climatic influence will remain the same, and (*iii*) climate change may alter the strength and extent of present climatic patterns (e.g., the sea breeze). A recent climate-induced decrease in area burned has been documented south of our sector (Bergeron 1991; Archambeault and Bergeron 1992; Bergeron et al. 2001); under a 2 × CO_2 climate scenario, global circulation models also agree with this trend (Bergeron and Flannigan 1995; Flannigan et al. 1998). If such a change were to occur, one would expect species ill-adapted to fire, such as white spruce, balsam fir, and to a certain extent black spruce, to gain importance in the study area. In light of our data, however, it is unclear how white spruce and balsam fir would behave in such a scenario because they seem to occupy rather restricted ecological niches in the James Bay sector (Gérardin 1980; Sirois 1997). On the other hand, with a climatic scenario conducive to more frequent fires, fire-adapted species such as jack pine would increase their importance locally and possibly expand their range.

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